

PSYCHOLOGY TEACHERS UPDATE

NO.11 - JANUARY 2006

ALTRUISM AND
HELPING BEHAVIOUR

KEVIN BREWER

ISSN: 1478-4548

Orsett Psychological Services
PO Box 179
Grays
Essex
RM16 3EW
UK

orsettpsychologicalservices@phonecoop.coop

PSYCHOLOGY TEACHERS UPDATE

Psychology Teachers Update is designed to give a brief overview of the main developments in the different areas of psychology. There is a proliferation of journals and research, and it is very difficult to keep abreast of the latest trends, particularly in the many and varied areas of psychology.

Each issue of Psychology Teachers Update will cover a particular topic, and summarise the main research directions and findings in the last ten to fifteen years approximately. The aim is to give teachers the feel of what is happening in that area of psychology.

AUTHOR

Kevin Brewer

Kevin is an experienced teacher of A level psychology since the 1980s. He has taught and examined with many of the different exam boards. He is a social psychology tutor with the Open University.

Author of three books published by Heinemann: "Psychology and Crime" (2000) and "Clinical Psychology" (2001) as sole author, and "Heinemann Psychology AS for AQA A" (2003) by David Moxon, Kevin Brewer, and Peter Emmerson. Kevin has published other material himself.

A complete list is available at
<http://kmbpsychology.jottit.com>.

PAST ISSUES

No.1 - September 2002: Memory

No.2 - January 2003: Evolutionary Psychology

No.3 - May 2003: Biological Psychiatry

No.4 - September 2003: Social Constructionism

No.5 - January 2004: Atypical Development

No.6 - May 2004: Issues in Health Psychology

No.7 - Sept 2004: Developmental Psychology

No.7 Supplement (No.1): Child Physical Abuse,
Neglect and Disadvantage

No.8 - January 2005: Children in Court

No.9 - May 2005: An Introduction to Psychoneuroimmunology

No. 10 - September 2005: Qualitative Psychology and
Research Methods

CONTENTS

	Page Number
INTRODUCTION	4
ALTRUISTIC BEHAVIOUR	4
Altruism as selfish behaviour	4
Altruism with kin	6
Direct reciprocity: altruism	
with non-kin	8
Other evolutionary explanations	9
Indirect reciprocity	11
Alternatives to evolution: social	
explanations	13
SOCIAL CO-OPERATION	14
Game theory and game-playing	14
Social co-operation and games	17
RECENT RESEARCH ON THE BIOLOGICAL BASIS TO ALTRUISM	26
CONCLUSIONS	26
FOOTNOTES	28
REFERENCES	30

Introduction

Altruism tends to be the term used when looking at evolutionary explanations for behaviour that benefits another at the provider's expense. Helping behaviour is more associated with social psychology (sometimes called pro-social behaviour), and is dominated historically by the work on bystander intervention. Co-operation is behaviour that is beneficial to all participants.

These behaviours are problematic:

Natural selection is conventionally assumed to favour the strong and selfish who maximise their own resources at the expense of others. But many biological systems, and especially human societies, are organised around altruistic co-operative interactions. How can natural selection promote unselfish behaviour? (Nowak and Sigmund 2005 p1291).

Altruistic behaviour is studied in different disciplines: evolutionary biology, social psychology, and economics.

Altruistic Behaviour

The donation of blood is a prime example of a behaviour that challenges the application of evolutionary principles to all human behaviour. Evolutionary principles suggest that individuals should be pre-occupied with survival, and with producing as many offspring as possible. Any behaviour that helps this will be enhanced by evolution, and any behaviour that limits it will die out.

Yet even among animals, there are examples of behaviour that appears to defy evolutionary explanation. Elliott and Gerritsen (2004) reported the case in New Zealand of dolphins protecting three teenage swimmers from a great white shark by herding around them for twenty minutes. Did the dolphins mistake the humans for young dolphins, or was it merely an instinct to herd vulnerable members at the appearance of a shark, as some suggested? Was it truly altruistic behaviour?

How is it possible to explain behaviour, like altruism, which goes against evolutionary principles?

ALTRUISM AS SELFISH BEHAVIOUR

One possibility is that the altruistic behaviour is an illusion, and, it is, in fact, selfish behaviour by

the individual.

An example comes from work with meerkats in South Africa. They live in communities where some animals watch for predators (guard) and give alarm calls, while others forage for food. The guards are assumed to be showing altruistic behaviour. Clutton-Brock et al (1999) challenged this idea. Based on over 2000 hours of observations, they noted that the animals guarding had already eaten, and were watching for predators for their own benefits. In other words, to see the predators first, and thereby reduce the personal risks.

However, the meerkat who sees the predator gives alarm calls to the others - this is altruistic behaviour. If the watchers were completely selfish, they would see the predator, make no alarm call, and quietly move themselves into the safety of their hole.

In a human example, Day (1998) quoted research from Finland that men who donated blood were less likely to have a heart attack (0.7% compared to 12% for non-donors). The benefits of donating blood were that it lowered iron levels and reduced the risk of a heart attack. Thus a definite selfish benefit of the altruistic behaviour of blood donation. However, these findings need to be treated with care as there may be many other reasons why the heart attack rate was lower for blood donors (eg: generally healthier lifestyle than non-donors).

There are too many examples among humans and animals of behaviour that is costly to the provider to explain all altruistic behaviour as really selfish behaviour in disguise.

Altruism as a by-product of mutual benefit

Hinde (1982) proposed the concept of mutualism where "two heads are better than one". For example, two unrelated birds defending a territory together benefits them both as it is easier than an individual bird alone.

Another common example, also used by birds among others, is the evolutionary benefits of adopting complete strangers. By gaining helpers to the family unit, this improves the survival of everybody in a rural society (Alcock 1993). Both sides benefit from the apparently altruistic behaviour.

In the case of lions, non-genetic males will unite to oust the dominant male from the pride. Subsequently, these males rarely fight over the females even though reproductive success may not be equally shared.

Males usually pair with two females, and this leaves

some males without mates. These "non-reproductive helpers" are useful in repelling rivals, but they do not mate. DNA fingerprinting of prides, by Packer et al (1990), has clearly shown that the helpers are not genetically related.

If they were genetic relatives, then it would seem obvious that defending your relatives will help your own genes indirectly. Bertram (1978) called this "reproducing by proxy through his companions".

The presence of helpers in the pride increases the survival rate by 0.64 cubs (Packer et al 1991), but only for those mating.

What are the advantages of the "non-reproductive helpers"? The simplest answer is their continued survival while in the group, which allows them the opportunity to mate later. This is not a convincing answer, though, in terms of evolution.

Emlen (1991) talked of the coalition formation hypothesis. The females in the pride come into oestrus simultaneously, and there are benefits to male coalition in terms of lifetime reproductive success.

Packer et al (1988) estimated the approximate lifetime reproductive success (ie: number of offspring fathered) of different size coalitions: one male can father five offspring, whereas with three males it becomes twenty, and for six males, thirty-five.

Overall, the advantage of the coalition is to make the pride take-over easier, and to increase the tenure time of controlling the pride.

ALTRUISM WITH KIN

Hamilton (1964) proposed the theory of kin selection (or inclusive fitness ⁽¹⁾) to explain altruistic behaviour towards kin, like a mother dying to save her offspring.

Dawkins (1976; 1989) reduced all behaviour to the survival of the gene rather than the survival of the individual. He proposed the Central Theorem of Extended Phenotype: "An animal's behaviour tends to maximum survival of genes 'for' that behaviour, whether or not those genes happen to be in the body of the particular animal performing it" (Dawkins 1989 p253).

A mother who dies to save three offspring will have saved one and a half times her own genes because each offspring carries half of the mother's genes ($3 \times \frac{1}{2} = 1\frac{1}{2}$). Though the mother dies, for Dawkins, it is the genes that survive, and evolution is about the continuation of the genes not the individual (ie: "the survival of the fittest genes"). Altruism is, thus, based on the degree of "genetic overlap" between individuals.

Dawkins (1989) used this example to show the principles of his idea. An individual finds eight items of food, but can only eat three. If each item of food is worth +6, selfishness produces a benefit of +18 (3 x +6). For the benefit of the genes, the individual could eat two items only and call three other animals to eat the rest: a brother (sharing half the same genes), a cousin (sharing 1/8), and unrelated animal (zero shared genes). This behaviour would give a total score of +19½, which is calculated thus:

Individual	2 food items x +6	= 12
Brother	2 x +6 x ½	= 6
Cousin	2 x +6 x 1/8	= 1½
Unrelated	2 x +6 x 0	= 0
	Total	+19½

For Dawkins, sharing, which appears as altruistic behaviour, is, in fact, beneficial to the individual's genes. If this is right, then animals should be altruistic towards closer kin than less related and non-related individuals.

Table 1 gives three examples of altruism towards close kin.

SOURCE	ANIMAL	RESULTS
Daly & Wilson (1983)	Japanese macaques	25% of time spent in mutual grooming between mother-offspring, only 4% for non-kin
Krebs & Davies (1993)	Black-tailed prairie dogs	50% of time alarm calls given by males when with offspring and only 25% for non-kin
Trivers (1985)	Belding ground squirrels	Average of 18 alarm calls towards daughter/grand-daughter compared to 5 when non-kin

Table 1 - Altruistic behaviour towards kin versus non-kin.

For example, among lions, males give cubs preference to food, females suckle any cub in the pride, and there is a lack of competition among males for females. All these behaviours appear to go against the logic of evolution. But when looking closer there is evolutionary logic to this apparent altruistic behaviour. The key is the genetic relationship of members of the same pride.

Bertram (1978) calculated that the average coefficient of genetic relationship between members of the pride to be 0.15 (15%) for females and 0.22 (22%) for

males. Thus males can be tolerant of cubs because of "inclusive fitness".

Altruistic behaviour will also take into account the costs and benefits of the behaviour. Hamilton (1964) explained the evolution of altruism based on kinship or benefits greater than costs of the behaviour. He produced mathematical models (figure 1).

Altruism occurs when: $K > 1/r$

$K = b/c$

KEY: c = cost of behaviour in terms of evolution

b = benefits of behaviour

K = ratio of costs to benefits

r = degree of kinship; eg: parent/offspring = 0.5

(After Clamp and Russell 1998)

Figure 1 - Mathematical model for apparent altruistic behaviour.

Simple experiments have been devised to show this type of altruism, like Fieldman et al (quoted by Walker 2001). Students were offered small cash rewards for performing skiing exercises, and the longer they performed the exercises the more money they received. The experimenters varied who would receive the reward.

Crouching in a skiing position was achieved on average for 120 seconds when the participants knew they would receive the money themselves. The average time was 80 seconds when the reward was to be given to a close relative sharing half their genes (parent, sibling) compared to 65 seconds for a cousin (sharing 1/8 same genes). The average time was much less when the rewards were going to non-kin friends.

But overall, altruism is always reduced by an increase in the costs to the individual (Fehr and Fischbacher 2003).

DIRECT RECIPROCITY: ALTRUISM WITH NON-KIN

Trivers (1971) proposed the idea of "delayed reciprocal altruism" to explain altruistic behaviour towards non-kin: "an exchange of altruistic acts between the same two individuals so that, in total, both obtain a net benefit". In other words, the idea of returning favours, or "tit-for-tat".

It is important that a relationship exists between the individuals involved, and there is an opportunity for a favour to be returned at a later date.

It has been argued that reciprocal altruism played a key role in the evolution of the brain (Crook 1980). The need to keep detailed mental records of who we owe and who owes us. Trivers (1985) saw the evolution of emotions like gratitude, sympathy, guilt, and shame as linked to "cheater-detection". Humans have evolved particularly good "cheating-detection" abilities (eg: face recognition of strangers who cheat in games) (Cosmides and Tooby 1992).

The evolution of mechanisms of social exchange meant that "cheater-detection" and "fairness" became important qualities. These developed into systems of justice (Krebs 1998). This is seen in concern not only about what happens to myself but also to third parties. Dunbar (1996) noted this latter concern in the evolution of gossip and language.

Reciprocal altruism is not that common in animals (Fehr and Fischbacher 2003). The concern for the welfare of others (ie: non-kin) (known as "other-regarding preferences"; Silk et al 2005) is not evident in chimpanzees, even with familiar individuals, and at no cost to the self, despite the fact that chimpanzees in the wild do collective activities like hunting.

Thus Silk et al (2005) had expected chimpanzees to show "other-regarding preferences". Using two groups of captive chimpanzees (in Texas and Louisiana), she and her colleagues offered individual chimpanzees the choice of food for themselves (known as 1/0) or food for themselves and another chimpanzee at the same time (known as 1/1). The choice of 1/1 did not vary whether another chimpanzee was present or not suggesting that the animals were not concerned with others (table 2).

	CHIMPANZEES:	
	LOUISIANA (n = 7)	TEXAS (n = 11)
CHOICE OF 1/1 WHEN ALONE	56	48
CHOICE OF 1/1 WHEN ANOTHER CHIMPANZEE PRESENT	58	48

Table 2 - Average percentage choices by chimpanzees.

But there are many occasions where humans will help others in a one-off situation with no possibility of the favour being returned. This is countered by the argument that the process works across society - you do a favour for a stranger, and another stranger will do favour for you later. This is known as "third-party altruism" (Trivers 1971) or "indirect reciprocity" (Alexander 1987). However, this does leave room for the "free

rider" (first level) to flourish (ie: those who never return favours). The "second level free-rider" co-operates, but does not join in the altruistic punishment of unco-operative individuals (Fehr 2004).

OTHER EVOLUTIONARY EXPLANATIONS

Nesse (1999) listed a number of ways that vulnerabilities to disease come from evolutionary thinking. Some of these are possibly applicable to altruism:

i) Defence - What is seen as a defect is, in fact, adaptive. Altruism is seen as weakness in evolutionary terms, but, in reality, has evolutionary benefits. This possibility has been covered earlier.

ii) "Design trade-offs" at level of gene - For example, two copies of the gene are adaptive, and one copy is maladaptive. This would mean there is a gene for altruism and another behaviour, and receiving one copy from each parent produces the other (evolutionary adaptive) behaviour. While to receive one copy produces altruism (2). Rachlin (2002) argued that what is inherited must be a general mechanism for altruism rather than to do specific altruistic acts.

iii) "Design trade-offs" at level of trait or behaviour - This means that the same behaviour, varied by matter of degree, produces either adaptive or maladaptive behaviour. For example, the adaptive version is helping kin, and the maladaptive version is the person who helps everybody.

Altruism as a evolutionary maladaptive behaviour

In this case, it could be that the behaviour no longer raises evolutionary fitness, but did in different environmental conditions. Crawford (1998) called this behaviour "pseudopathological".

During the first appearance of humans (approximately 200 000 years ago; Laland and Brown 2002), there were evolutionary benefits to altruism, say in the small groups that lived together (and were probably mostly kin), but the benefits are lost today as we live in larger societies with non-kin. For example, Symons (1979) estimated that infant mortality could be as high as 65% in early human society, so any help would reduce this.

Another example is helping strangers in an avalanche: the "evolutionary brain" helps because it "thinks" the strangers are kin (Crawford 2002).

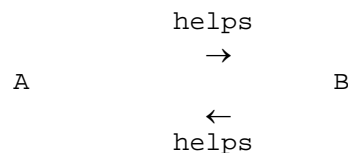
Another possibility is that altruism is a maladaptive by-product of another behaviour. For example, families of white whales will adopt non-kin, and this can be seen as the maladaptive by-product of their motivation to have offspring, particularly if the family has lost a calf in the past (Bremmer 1986).

On the other hand, altruism may be "true pathology" (Crawford 1998) in that it is a behaviour that is detrimental in both ancestral and current environments. But, if this is the case, it would be expected to have died out (ie: genetically) if altruists kept "sacrificing" themselves for others. Unless there is some other benefit (in genetic terms) from being an altruist (3).

INDIRECT RECIPROCITY

Direct reciprocity is the principle of "you scratch my back and I'll scratch yours", while indirect reciprocity can be summed up as "you scratch my back and I'll scratch someone else's" ("upstream reciprocity") or "I'll scratch your back and someone else will scratch mine" ("downstream reciprocity") (Nowak and Sigmund 2005) (figure 2).

DIRECT RECIPROCITY



INDIRECT RECIPROCITY

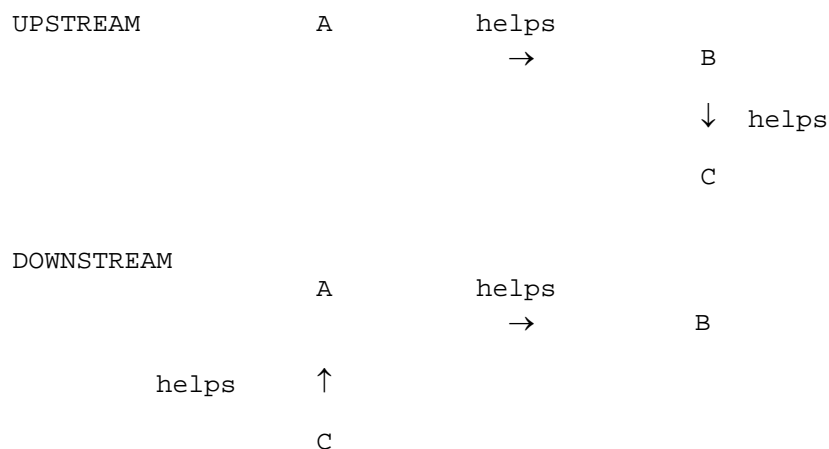


Figure 2 - Direct and indirect reciprocity.

Is indirect reciprocity a "misdirected act of gratitude"? "In one case recipients are thanked for what another did; in the other case recipients are thanked by someone who did not profit by what they did" (Nowak and Sigmund 2005).

A key component of indirect reciprocity is reputation (Nowak and Sigmund 1998; Milinski et al 2002). "Downstream reciprocity" can be explained in this way: C helps A because of A's reputation for being altruistic.

Fehr and Renninger (2004) felt that it was "generally advantageous to establish a reputation for benevolence and impartiality through the use of well-targeted good deeds" (p17).

Alexander (1987) argued that a blood donor shows to others that they are a "good person" - a desirable person to include in the group, or even a sign of a potentially "good mate". In other words, "if I am willing to give blood to strangers, then I will be helpful in the upbringing of our offspring".

Nowak and Sigmund (1998) argued that reputation replaced genetic relatedness to explain altruism in small populations of early humans. Co-operation by indirect reciprocity thrives in populations where everybody knows everybody else's reputation. But reputation does not seem to be important, in the same way, among animals (Fehr and Fischbacher 2003).

Explanations for the evolution of reputation include "costly signalling" (Zahavi 1995) or cultural group selection (Gintis et al 2001). The former idea is that animals which handicap themselves, like the peacock's tail, signal how good their genes that they can survive with such a handicap. Thus co-operating, and the personal cost, can be borne by the individual because their genes are so good. The latter idea is a variation on group selection theory (ie: natural selection works on a species' group as a whole).

Reputation has risks: the donor's action or intention may be interpreted differently by different people; and how the reputation is communicated to others, through gossip, say, could provide conflicting information. "The reputation of a person is therefore not simply a label that is visible to all others, but instead each person has a private list of the reputation of others" (Nowak and Sigmund 2005).

The reputation argument can be applied for many "culturally-approved" behaviours. "Reputation mechanisms" exist in all societies from medals for heroic acts to satisfaction scores on "eBay" (nowak and Sigmund 2005).

In evolution, it should hold strongest for men in terms of sexual selection.

Bolton et al (2005) varied the amount of information known about co-players, in a co-operative game experiment, from (a) none; (b) behaviour in last round; (c) to full details of playing history. More information about past co-operation and selfishness enhanced co-operation in the game.

Game-players seemed to be aware of reputation for generosity because donations (co-operation) were more frequent in earlier rounds of the game. Thereby establishing a good reputation. But this generosity can still exist even when individual reputations are not communicated to other players (Nowak and Sigmund 2005).

Engelmann and Fischbacher (2002 quoted in Fehr and Fischbacher 2003) allowed half the game players to gain a reputation from past rounds of the game, and the other half not. In the first case, 74% of individuals co-operated compared to 37% for the latter. But co-operators do not want a reputation as "push-overs". Players who had good reputation from past games asked for more reward than in games where reputation was not included (Fehr and Fischbacher 2003).

Milinski et al (2002) felt that in real life individuals often participate in several "social games" simultaneously. The researchers found that reputation was still important even when the games played were alternated.

Reputation theory has been applied to real-life food-sharing among the Ache in Paraguay (Gurven et al 2000).

Thus, in real life, it should be expected that donors would want to publicise their charity with a badge, say. This still leaves anonymous and secretive donations to be explained.

ALTERNATIVES TO EVOLUTION: SOCIAL EXPLANATIONS

Evolution may not be able to explain all human behaviour. Alcock (1993) admitted that it was quite possible that some human behaviour would have "violated expectations derived from evolutionary theory, especially since so many human actions.. are very recent cultural phenomena" (p547).

Gintis (2003) argued for gene-culture co-evolution of altruism. This is where evolutionary principles become institutionalised in society. This allows for cultural differences: for example, the Hazda (Tanzania) use altruistic punishment for individuals who do not co-

operate with the group, while it is not so for the Machiguenga (Peru) (Fehr and Fischbacher 2003).

Bystander Intervention

Lippa (1994) defined bystander intervention as a "quick response to sudden danger that endangers another and may sometimes place the helper in considerable danger". In other words, helping the victim rather than general helping in society. Explanations for bystander intervention tended to focus upon the situational determinants of helping or not helping.

Bystander intervention is dominated by the work of Latane and Darley (1970) including their Decision Model of Emergency Intervention, and Piliavin et al's (1981) "Subway Samaritan" studies and Exchange Theory. The former model explored the stages and factors in the decision to help, while the latter included an assessment of the costs of helping and not helping, and the rewards.

The early research focused upon the cognition of helping - thinking and decision-making processes, while recent work looked at the emotions involved. Batson (1991) developed the empathy-altruism hypothesis where altruistic behaviour is based on feeling empathy for the victim. The model is supported by research that showed that when empathy is high, participants will help whether there is anticipated continued exposure to the suffering of the victim or not. Selfish motives would mean helping only if exposure to the victim's suffering was inescapable (Batson 2000).

Social Co-operation

GAME THEORY AND GAME-PLAYING

Altruism and co-operation have been studied using game-playing and game theory. Research makes use of three types of games:

i) Public good games (or mutual aid games) - all players give money towards common project. Selfishness is giving as little as possible, and co-operation is giving as much as the other players. Experimental evidence still holds with real money, and large amounts (eg: three months' income) (Fehr and Fischbacher 2003);

ii) Ultimatum games - players have a forced choice between two options of co-operating or being selfish; eg: prisoner's dilemma;

iii) Trust games (or gift exchange games) - one player gives money to another player, and trusts that they will give back a similar amount. Selfishness is the recipient not giving back money, and co-operation is giving back as much as received.

Game theory is a mathematical principle that has also been applied in biology to explain animal behaviour, from aggression to altruism (Maynard Smith 1974; 1982). A key concept is the evolutionary stable strategy (ESS), which is the strategy, if most members of a population adopt, that cannot be bettered. An individual's strategy will depend upon the population strategy.

So, for example, if an ESS is co-operation, then an individual strategy of selfishness could work in the short-term, but co-operation would be better in the long-term. On the other hand, an ESS of selfishness would make co-operation a bad idea for an individual. Mathematical models are designed using game theory, and they vary the costs and benefits of certain behaviours (4).

Panchanathan and Boyd (2004) set up a "mutual aid game" which involved a "needy" player and whether the other players would help the "needy" player at their personal cost. Four strategies were possible in this type of game:

- i) "Co-operators" - help all "needy" players;
- ii) "Defectors" - do not help at all;
- iii) "Shunners" - help "needy" players of good reputation from past games (ie: "co-operators"), and not those of bad reputation ("defectors");
- iv) "Reciprocators" - help "needy" players based on reputation from current game.

The first two strategies are known as "unconditional strategies" (ie: strategy not changed by behaviour of others), and the latter two are "conditional strategies".

The researchers used mathematical modelling to establish the ESS. They concluded that "shunners" produced the best long-term co-operation within a group that remained together.

So the amount of contact is key. In a one-off encounter, selfishness or defection is the best strategy, but in a series or continued encounters, it is co-operation with reciprocation or shunning that is the best for the individual and the whole group. Thus it is possible to explain altruism and co-operation with non-

kin as a calculation of costs and benefits as proposed by game theory.

Any group of altruists is at risk of exploitation from "egoists", except that: "When an egoist immigrated to a group inhabited by altruists, he was probably punished for his actions by the altruists who did not care whether they derived personally and from their action" (Fehr and Renninger 2004 p21).

Also, a population of "egoists" will lose out to "retaliators" (Nowak et al 2004). It is the overall payoff that matters not the individual encounter. A "retaliator" would be exploited in the first encounter by an "egoist", but would compensate with altruistic exchanges with other "retaliators". This co-operation, in the long-term, would mean that "retaliators" benefit more than "egoists" with their selfish behaviour (5).

But Brann and Foddy (1988) found cases of individuals who continued to co-operate in games regardless of the behaviour of the other players. Rachlin (2002) explained this behaviour as the individuals having "decided to co-operate in life and continue to do so in the experiment, not necessarily because of some innate tendency to be altruistic, but because altruism is generally valuable and they would not act altruistically if they made decisions on a case by case basis". This has important implications for those who believe experiments take place in a vacuum.

Rachlin (2002) focused on the example of a woman running into a burning building to save someone else's child. He argued that such an act "forms part of a pattern of acts in her life, a pattern that is valuable in itself, apart from the particular acts that compose it" (p240). In other words, altruistic behaviour is "a kind of habit".

Put another way, any behaviour is in the context of other behaviours: "to choose to be an altruistic person". "But in order to pattern our behaviour in this way.. we must forego making decisions on a case-by-case basis" (Rachlin 2002).

"Game theory" has been criticised for being static and based on one game at a time, whereas real life situations are dynamic with players looking ahead to see what the opponent might do. This has led to variations like "Theory of Moves" (Matthews 2000).

SOCIAL CO-OPERATION AND GAMES

The social order and stability of modern society is based upon the co-operation of genetically unrelated individuals. The prevailing view is that individuals co-operate out of self-interest because of the reward for doing so or sanctions for not co-operating. In the main, we are talking about trust. This is the basis of modern economic exchange.

Here researchers talk about "altruistic co-operators", who "are willing to co-operate, that is, to abide by the implicit agreement, although cheating would be economically beneficial for them" (Fehr and Rockenbach 2003 p137).

Fehr and Renninger (2004) summed up the situation: "Like many members of the animal kingdom, people will readily lend a hand to immediate family and relatives. But humans alone extend altruism beyond kin, frequently helping perfect strangers for no obvious personal gain" (p15).

Ultimatum Games

Fehr and Fischbacher (2003) used a typical design of ultimatum games in their experiments. Two players must agree on sharing of money: player A proposes and player B accepts or rejects. If B rejects, then both players receive zero, but they keep the money if they agree. Respondents tend to reject offers if their share is below 25%. Proposers who are rejected in the previous round increase their offer next time by an average of 7% even if each of ten rounds is played with different people.

In the "dictator game", player B has no say and must accept whatever is given.

Fehr and Fischbacher (2003) introduced a variation with a judge of fairness (player C). Player A has 100 MUs (monetary unit) to allocate, and player C can fine A for unfair distribution. But any fines imposed by C reduce their 50 MUs. Thus there is a cost to C if they punish the unfairness of A. If A gives less than 50 MUs to B, C will punish 55% of the time, and the lower the donation, the higher the fine imposed by C (table 3).

AMOUNT TRANSFERRED BY PLAYER A (MU)	AMOUNT OF FINE IMPOSED BY PLAYER C (MU)
0	14
10	10
20	8
30	5
40	3
50	0

Table 3 - Approximate amount of fines based on amount transferred by player A.

Prisoner's Dilemma

The original game designed to study co-operation was "prisoner's dilemma" (Axelrod 1984). In the basic scenario, two prisoners are kept separately (without communication), and each must decide whether to confess to the police (known as defecting) or keep quiet (known as co-operating). There are different lengths of prison sentence depending on who defects or not. Usually this scenario is now played with points gained as in figure 3.

	PLAYER B CO-OPERATE	DEFECT
PLAYER A		
CO-OPERATE	5 5	6 1
DEFECT	1 6	2 2

Figure 3 - Payoff matrix of prisoner's dilemma game.

When prisoner's dilemma is played over a series of rounds, the strategy known as "tit-for-tat" produces co-operation between the players. "Tit-for-tat" involves copying the other player's last strategy - if they defected in the last round, you defect this round, or if they co-operated last time, you co-operate this round. In effect, defection is punished, and this produces the stability of co-operation. But mistakes between two players using this strategy can lead to "mutual backbiting" (Nowak and Sigmund 1993).

Co-operation in prisoner's dilemma-type situations can be seen in the use of mediation and compromise in conflict situations. Howley (2002) quoted this case study from Bougainville in south-east Asia:

Denis stole timber from the Peter's shed. Denis pointed out that although Peter owns the chainsaw, Denis

provided the petrol for it, and was thus entitled to the timber. This was producing conflict between them and their families. Mediation helped them to agree that Denis could buy the timber at half price.

Figure 4 shows the benefits of co-operation.

		PETER	
		CO-OPERATE	NOT CO-OPERATE
DENIS	CO-OPERATE	no conflict; buy timber at half price	Denis unhappy and leads to timber theft
	NOT CO-OPERATE	Peter unhappy as timber stolen and refuse use of chainsaw	violent conflict develops

Figure 4 - Prisoner's dilemma matrix for Denis and Peter's dispute.

Co-operation in prisoner's dilemma games can be influenced by prior communication between the players, and by computers always playing the same strategy or playing randomly (Silverstein et al 1998). Playing prisoner's dilemma with a computer has been used in a number of experiments.

Baker and Rachlin (reported in Rachlin 2002) compared students playing against computers that were programmed to follow a "tit-for-tat" strategy or a "Pavlov" strategy (Nowak and Sigmund 1993). The "Pavlov" strategy involves the computer's current choice being repeated on the next trial if the student co-operates or changed if the student defects. Figure 5 shows the difference between the two strategies.

The students played 100 trials, and either knew they were playing a computer or believed it was another student. Despite the same strategies being used by the computer, the students behaved differently (table 4).

"TIT-FOR-TAT" STRATEGY

- computer repeats student's last decision

	STUDENT	COMPUTER	STUDENT	COMPUTER
Round 1	C	C	D	C
Round 2		C		D

"PAVLOV" STRATEGY

i) computer changes choice if student defects

	STUDENT	COMPUTER	STUDENT	COMPUTER
Round 1	D	C	D	D
Round 2		D		C

ii) Computer keeps same strategy if student co-operates

	STUDENT	COMPUTER	STUDENT	COMPUTER
Round 1	C	C	C	D
Round 2		C		D

C = co-operation; D = defection

Figure 5 - Different strategies used by the computer.

COMPUTER STRATEGY	"Tit-for-Tat"	"Pavlov"
Student knew playing computer	75	35
Student believe playing another student	35	65

(After Rachlin 2002)

Table 4 - Approximate mean percentage of co-operate choices by students in last fifteen trials.

But individuals are not always logical. Matthews (1998) quoted the idea of "drama theory" which is irrational or emotional behaviour applied to these game scenarios. In a real prisoner's dilemma situation, if one person is an unwilling accomplice than "drama theory" predicts a "save own skin" strategy and defect.

"Drama theory" has also been applied to the scenario of "chicken" (two cars driving at each other to see who swerves away first). "Game theory" predicts different

results compared to "drama theory" (figure 6).

"GAME THEORY"			"DRAMA THEORY"		
PLAYER B			PLAYER B		
SWERVES	DRIVES ON		SWERVES	DRIVES ON	
PLAYER A			PLAYER A		
SWERVES	3/3	2/4	SWERVES	5/5	2/4
DRIVES ON	4/2	1/1	DRIVES ON	4/2	4/4
Both swerve (ie: co-op) makes sense (3 pts each)			Because of emotions, co- operation is stronger (5 pts each), but so is irrational behaviour of both driving on and crashing (4 pts each)		

Figure 6 - Payoff matrices for the game of "chicken".

Rachlin (2002) used a more complex game based on the principles of prisoner's dilemma. Ten players are given a choice between "Y" and "X" where:

1. If you choose "Y", you get 100 x "N";
2. If you choose "X", you get 100 x "N" + 300;
3. "N" is the number of people (out of ten) who choose "Y".

A selfish strategy would be to choose "X", because even if nobody else chooses "Y" (and thus "N" = 0), you still gain 300. But complete co-operation (ie: everybody chooses "Y") would give each player 1000 ("N" = 10 x 100).

Rachlin found similar results from different groups, including Italian economists, Japanese psychologists, and US undergraduates, that about half group chose "X" and half "Y". Selfishness leads to greater earnings. Those who chose "Y" received 500 ("N" = 5 x 100), and those "X" got 800 ("N" = 5 x 100 + 300).

But when Rachlin phrased the game in terms of the money won going to a common good, then co-operation increased.

This example is typical of "primrose-path experiments" (eg: Herrnstein 1991). But usually the players are told less or nothing at all about the rules, and "N" is calculated at the end of a number of trials.

Interestingly, if the rounds of the game are played quickly one after another, co-operation was greater than playing one round followed by a break before the next round (Kudadjie-Gyamfi and Rachlin 1996).

Public Good Games

In "public good games" (6) where individuals co-operate for the benefit of all, they initially contribute 40-60%, but co-operation declines because of "free-riders" (Dawes 1980). Research has shown that certain strategies exist. One is "conditioned co-operation" where the player co-operates because they believe others will. Then there is the "strong reciprocator" who rewards fair behaviour (co-operation by others) and punishes unfair behaviour (selfishness) even to their own costs (Fehr and Rockenbach 2004).

Fehr and Gächter (2000) introduced the opportunity to punish other group members for not co-operating at cost to the self. This increased co-operation to 65%, and later 100%, compared to co-operation without punishment which peaked at 55% but went down to 10% at the lowest point.

These researchers also found that 74.2% of acts of punishment on "defectors" (below-average contributors) were by "co-operators" (above-average contributors), and the larger the defection the greater the punishment. For example, individuals who contributed by up to 20 MUs less than the rest of the group were more likely to receive the maximum fine of 10 MUs. Remember that the punishment comes out of the profit of the players doing the punishing. The participants were undergraduates at two Swiss universities.

This idea of fairness has been called "inequity aversion" (Fehr and Schmidt 1999). It is not universal. Henrich (2004) found it in five societies, not in three, and seven others unsure. There is also debate about this behaviour in brown capuchin monkeys (*Cebus apella*) (Brosnan and de Waal 2003 say, and Henrich 2004 disagrees).

Fehr and Renninger (2004) set up a "public good game" with four participants each given 20 MUs. The players were asked to invest in a project for the public good any amount they wanted. The group were allowed to punish individuals with fines who did not give an equal amount to the project (co-operate). Each group played ten rounds. Table 5 shows that punishing those not co-operating produced greater contributions by all members when the groups were stable compared to changing groups each round.

This research showed "that many people - even when facing high monetary stakes are willing to penalise others at a cost to themselves to prevent unfair outcomes or to sanction unfair behaviour" (Fehr and Renninger 2004 p18).

	ROUND 1	ROUND 10
Stable group with punishment	12	18
Changing group with punishment	11	11
Changing group without punishment	8	2

Table 5 - Approximate average contribution by group members (out of twenty MUs).

There is a difference between "strong or true altruism" which punishes the free-rider at own expense, and "weak or false altruism" which anticipates later payback (Fehr and Renninger 2004).

Boyd et al (2003) statistically modelled group size and co-operation (table 7). Punishment of defectors and of those who do not punish defectors ("second level free-riders") produces the best levels of co-operation.

	CO-OPERATION BREAKS DOWN	GOOD LEVEL OF CO-OPERATION
No punishment of defectors	16	50% at 12
Punishment of defectors	128	40% at 32
Punishment of defectors and those who do not punish defectors	none	70-80% up to 512

Table 7 - Statistical modelling of group size and co-operation levels.

Also there is the role of reputation. If a co-operating individual (A) decides not to co-operate to punish a selfish individual (B), does that not reduce the reputation of A as a co-operator? But if A continues to co-operate with B, again the reputation of A may not be enhanced, and the society may be destabilised (Nowak and Sigmund 2005).

Through mathematical modelling, Ohtsuki and Iwasa (quoted in Nowak and Sigmund 2005) found that an individual of good reputation can refuse to help one of bad reputation without harming the former's reputation (known as "justified defection").

Moreover, players who justifiably refuse to donate to a defector show an increased tendency to provide donations in the following rounds, as if to make up for their refusal. This indicates

that they expect their refusal to lower their score in co-players' eyes and that they do not rely on the community's understanding
(Nowak and Sigmund 2005 p1296).

But Fehr and Rockenbach (2003) showed that sanctions for selfish behaviour/cheating far from encourage altruism, and, in fact, altruistic co-operation breaks down.

In this trust game, two anonymous participants are playing for money with one participant as the "investor" (Iv), and the other as the "trustee" (T). Iv decides to invest a certain amount of money, and T can "honour" that (known as "back-transfer"), and both players benefit.

However, T could keep Iv's investment (cheating), and T benefits at the expense of Iv. But if Iv does not trust T, then Iv can choose to invest the minimum (ie: 0). In this case, both players keep their initial stake given by the experimenters, and that is the only gain.

The conditions of the game are varied throughout the experiment. Figure 8 shows the basic rules of the game.

SITUATION		OUTCOME
co-operation	Iv invests 10 MU/ T "honours" 10	Both players receive 15 from experimenter (profit = 5 ie: 15-10)
T cheats	Iv invests 10/ T does not "honour" 0	T gains 10 profit, Iv loses 10
I does not trust	Iv invests 0/ T 0	both players receive zero

(MU = monetary units)

Figure 8 - Basic rules of the game.

Fehr and Rockenbach devised two experimental variations of the game - the trust condition, and the incentive condition:

i) Trust condition - Basic rules of the game (7), and no sanctions against cheating by T. This is the baseline measure of co-operation;

ii) Incentive condition - Iv can choose to fine T who does not co-operate. T knows before making a decision whether the fine will be imposed.

Each pair of participants played once to avoid reputation formation. Altruistic co-operation was

measured as T honouring Iv's investment when no fine was to be imposed. The first experiment involved twenty-four pairs of participants in the trust condition, and forty-five pairs in the incentive condition. While the second experiment used fifty more pairs in the incentive condition. This was a total of 238 students from the University of Bonn in Germany.

The results of the first experiment showed that 79% of T in the trust condition paid some money. In the incentive condition, "back-transfers" by T were highest when Iv chose not to impose the fine, and lowest when a fine was imposed (table 6). The main finding was that the imposition of the fine reduced co-operation, which goes against the "selfish interest" view of altruistic co-operation.

	TRUST CONDITION	INCENTIVE FINE CHOSEN	CONDITION NO FINE CHOSEN
Numbers of observations (pairs)	24	30	15
Actual back-transfer (MU)	7.8	6.0	12.5

(After Fehr and Rockenbach 2003)

Table 6 - Average payoff in first experiment.

One point to note is that Iv tended to invest more in the incentive condition: no fine chosen (8.7 vs 6.5 in trust condition), and generally T gave back more for higher investments. However, calculation of the actual back-transfers as a percentage of the investment were still significantly in favour of the incentive condition: no fine chosen.

So the next question is why did so many Iv threaten to impose a fine when the returns were poorer. The second experiment set out to answer this question with two possible hypotheses - the Iv did not realise the back-transfers would be less, or they chose to forego money to impose a fine on the perceived unfair behaviour of T (ie: the principle of punishing cheating behaviour).

The Iv was told, at the beginning of the experiment, that fining produced lower back-transfers. Even so, 68% of Iv preferred to fine cheating T. This supports the hypothesis that it was the principle of punishing cheaters that mattered.

Another question is why did the T pay back more when the fine was waived. It could be that imposing the fine was perceived by T as a hostile act. Thus the punishment

of the fine was perceived as serving the punisher's self-interest. But in "public good" experiments, where co-operation is beneficial to a whole group, sanctions enhance co-operation.

Recent Research on the Biological Basis to Altruism

Recent research has attempted to study game players while brain scanning them. For example, Sanfey et al (2003) found that specific areas of the brain were activated, using functional magnetic resonance imaging (fMRI), when nineteen participants were playing a bargaining game.

When faced with an unfair offer, three areas of the brain became active: bilateral insula (associated with emotions), the dorsolateral prefrontal cortex (DLPFC), and the anterior cingulate cortex (ACC) (both involved in executive and cognitive tasks). If the bilateral insula was more activated than the DLPFC, the individual would reject the offer, but the other way around, they would accept it.

Rilling et al (2002) also used fMRI, but with players of prisoner's dilemma. Mutual co-operation with human players produced activity in the "reward circuits" of the brain (mesolimbic dopamine system including the striatum and orbitofrontal cortex). But there was no activation here when co-operating with computer players or human players defecting.

In terms of biochemistry, there is interest in the hormone oxytocin, which is known to be involved in maternal attachment (eg: Insel and Young 2001). Kosfeld et al (2005) used a trust game where one player invests up to 12 MUs, and the trustee can back-transfer as much as they wish. Twenty-nine players were injected with oxytocin, and twenty-nine with a placebo. Co-operation was greater with the oxytocin group (average back-transfers of 9.6 MUs vs 8.1 for placebo group).

In another condition where the trustee's decision was done randomly, oxytocin has no effect (average back-transfers of 7.5 MUs for both groups).

Conclusions

There are different types of altruism, helping, and pro-social behaviour which have different motivations. For example, co-operation in games to take less money for the benefit of all can be seen as a form of self-control

(Rachlin 2002).

The different motivations for pro-social behaviour can be seen in this example of four soldiers (Rachlin 2002) who are ordered to advance on the enemy. Two soldiers advance and two do not:

a) Soldier A advances because just obeying orders, and fears the consequences of disobedience;

b) Soldier B advances because of the belief in the cause or the patriotic duty to do so;

c) Soldier C does not advance because of the personal costs far outweighing the benefits or the costs of disobedience;

d) Soldier D does not advance because of the immorality of the orders.

People help others for good and bad reasons. Helping can have a great effect upon the self. In a Japanese study, Yagi and Shimuzu (1996) found that individuals whose self-esteem was threatened used helping behaviour to restore their self-esteem. Participants were given an opportunity to help in volunteer projects after a "failure task" (a task that the individual could not do; eg: unsolvable puzzle).

The control group, without the task, averaged 5.81 days volunteering. Those participants whose self-esteem was lowest from the "failure task" offered an average of 16.75 days of volunteering.

Table 7 lists possible selfish motives for helping others.

- Material reward; public praise; non-tangible reward (eg: in after-life)
- Reduce distress of seeing other's suffering
- Escape guilt and shame of not helping
- Feel good about self for helping (bolster self-esteem)
- To gain an advantage or power over another
- Misjudged situation and not realised risk

Table 7 - Selfish motives for helping others.

Dovidio and Penner (2003) ended their review on altruism and helping with a conceptual model that attempted to integrate the different explanations (figure 9).

Thus:

In conclusion, although many manifestations of helping, particularly those that are commonly studied in the lab, appear simple and straightforward, helping is a complex multidetermined behaviour

(Dovidio and Penner 2003 p186).

FORM OF HELPING

- either direct or indirect; short or long-term; action or inaction

↑

GOALS/MOTIVES

- egoistic/selfish or altruistic motives

↑

SITUATIONAL/SOCIAL/PERSONALITY FACTORS

- including costs of helping; social norms; and personality characteristics; eg: trait of "Other-Oriented Empathy"

↑

COGNITIVE/AFFECTIVE PROCESSES

- including learning to help during socialisation; the emotion of empathy; and moral reasoning

↑

EVOLUTIONARY PROCESS/INCLUSIVE FITNESS

- helping was beneficial to early humans, and is reflected in "pro-social genetic predispositions among contemporary humans"; both helping kin, and non-kin in process of reciprocity

(After Dovidio and Penner 2003)

Figure 9 - Conceptual model in helping and altruism.

Footnotes

1. Inclusive fitness can be defined as "an individual's reproductive success" and "the extra reproductive success its relatives had because of its behaviour, devalued.. by the coefficient of relatedness of the relative" minus "the extra offspring the individual had.. because of the help it received from its relatives" (Grier and Burk

1992).

2. The "parent of origin effect" means that a gene can also have a different effect depending on the parent of origin. For example, the absence of certain genes on maternal chromosome 15 leads to Angelman syndrome (eg: spasms, "puppet-like" movements, and low intelligence), while absence of the same genes on the paternal chromosome 15 causes Prader-Willi syndrome (which includes the symptoms of obesity, and low intelligence) (Craddock and Owen 1996).

3. A similar idea has been proposed for the concept of the "gay gene". An evolutionary contribution could be that homosexual individuals are particularly good at helping heterosexual relatives (LeVay 1993).

4. Computer simulations of population behaviour includes Nowak and Sigmund (1993; 1998).

5. Using the payoff matrix in figure 3, player A is an "egoist" and always defects, while the "retaliator" is player B and co-operates. In the first encounter, A gets 6 points and B 1 point. But subsequently player A only meets other defectors, and thus only gets 2 points each time. In further rounds, player B meets co-operators, and thus always gets 5 points each time.

6. "Public good" games came from an article by Hardin (1968) entitled "The tragedy of the commons". It used the scenario of farmers who shared a common grassland for their cows. If each farmer expands their herd, which is profitable, the grass will be eaten. So it is necessary for the farmers to limit the size of the herd (co-operation). This is also true in real life examples like the fish stocks in the North Sea (Pennington 1999).

Messick et al (1983) were the first to devise an experimental version of the commons situation. A group of six players start with a pool of 300 points and the aim is to accumulate individually as many points as possible, but the players must make the game last as long as possible as well. Each player can take up to ten points in each round, and the pool is replenished by 10% after each round.

The selfish behaviour of each player taking the maximum means the game is over in six rounds, whereas co-operative behaviour, in the long-term, produces greater profits for all (table 8).

SELFISH STRATEGY: Each
of 6 players takes 10 pts
every round

CO-OPERATIVE STRATEGY: Each
of 6 players takes 5 pts every
round

ROUND	TOTAL BEFORE	TOTAL AFTER	10% REPLENISH	TOTAL BEFORE	TOTAL AFTER	10% REPLENISH
1	300	240	24	300	270	27
2	264	204	21	297	267	27
3	225	165	17	294	264	27
6	83	23	3	284	254	26
12	-	-	-	251	221	23
18	-	-	-	194	164	17
26	-	-	-	46	16	2
GAME TOTAL PER PLAYER = 60				GAME TOTAL PER PLAYER = 130		

Table 8 - Selfish and co-operative strategies.

7. The exact procedure involved giving participants 10 MU (1 MU = 0.5 DM) at the beginning of the experiment. The Iv could invest between zero and ten MUs as preferred. Whatever was invested was tripled for the T. The Iv would also specify a "desired back-transfer" (ie: how much they would like back). The T was free to give any amount back including the "desired back-transfer". In the incentive condition, the fine was 4 MUs.

References

- Alcock, J (1993) Animal Behaviour (5th ed), Sunderland, MA: Sinauer Associates
- Alexander, R.D (1987) The Biology of Moral Systems, New York: Aldine de Gruyter
- Axelrod, R (1984) The Evolution of Co-Operation, New York: Basic Books
- Batson, C.D (1991) The Altruism Question: Towards a Social-Psychological Answer, Mahwah, NJ: Erlbaum
- Batson, C.D (2000) Altruism: Why do we help others? Psychology Review, September, 2-5
- Bertram, B.C.R (1978) Kin selection in lions. In Bateson, P & Hinde, R (eds) Growing Points in Ethology, New York: Cambridge University Press
- Bolton, G.E; Katok, E & Ockenfels, A (2005) Co-operation among strangers with limited information about reputation, Journal of Public Economy, 89, 1457-1468
- Boyd, R; Gintis, H; Bowles, S & Richerson, P (2003) The evolution of altruistic punishment, Proceedings of the National Academy of Science of America, 100, 3531-3535
- Brann, P & Foddy, M (1988) Trust and consumption of a deteriorating common resource, Journal of Conflict Resolution, 31, 615-630

- Bremmer, F (1986) White whales on holiday, *Natural History*, 95, 40-49
- Brosnan, S.F & de Waal, F.B.M (2003) Monkeys reject unequal pay, *Nature*, 425, 297-299
- Clamp, A & Russell, J (1998) *Comparative Psychology*, London: Hodder & Stoughton
- Clutton-Brock, T et al (1999) Selfish sentinels in co-operative mammals, *Science*, 4/6, 1640-1644
- Cosmides, L & Tooby, J (1992) Cognitive adaptations for social exchange. In Barkow, J; Cosmides, L & Tooby, J (eds) *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, Oxford: Oxford University Press
- Craddock, N & Owen, J (1996) Modern molecular genetic approaches to psychiatric disease, *British Medical Bulletin*, July, 434-452
- Crawford, C (1998) Environments and adaptations: Then and now. In Crawford, C & Krebs, D (eds) *Handbook of Evolutionary Psychology: Ideas, Issues and Applications*, Mahwah, NJ: Lawrence Erlbaum
- Crawford, C (2002) on: Hero Factor: Cry of the Wild, Discovery Channel
- Crook, J (1980) *The Evolution of Human Consciousness*, Oxford: Oxford University Press
- Daly, M & Wilson, M (1983) *Sex, Evolution and Behaviour* (2nd ed), Belmont, CA: Wadsworth
- Dawes, R.M (1980) Social dilemmas, *Annual Review of Psychology*, 31, 169-193
- Dawkins, R (1976) *The Selfish Gene*, Oxford: Oxford University Press
- Dawkins, R (1989) *The Selfish Gene* (2nd ed), Oxford: Oxford University Press
- Day, M (1998) Give blood, live longer, *New Scientist*, 17/10, p15
- Dovidio, J.F & Penner, L.A (2003) Helping and altruism. In Fletcher, G.J & Clark, M.S (eds) *Blackwell Handbook of Social Psychology: Interpersonal Processes*, Oxford: Blackwell
- Dunbar, R (1996) *Grooming, Gossip and the Evolution of Language*, Cambridge, MA: Harvard University Press
- Elliott, J & Gerritsen, J (2004) More than just a pretty face, *Sunday Times*, 28/11, p14
- Emlen, S (1991) Evolution of co-operative breeding in birds and mammals. In Krebs, J & Davies, N (eds) *Behavioural Ecology: An Evolutionary Approach*, Oxford: Blackwell
- Fehr, E (2004) Don't lose your reputation, *Nature*, 432, 449-450
- Fehr, E & Fischbacher, U (2003) The nature of human altruism, *Nature*, 425, 785-791
- Fehr, E & Gächter, S (2002) Altruistic punishment in humans, *Nature*, 415, 137-140
- Fehr, E & Renninger, S-V (2004) The Samaritan paradox, *Scientific American Mind*, 1, 14-21
- Fehr, E & Rockenbach, B (2003) Detrimental effects of sanctions on human altruism, *Nature*, 137-140
- Fehr, E & Rockenbach, B (2004) Human altruism: Economic, neural and evolutionary perspectives, *Current Opinion in Neurobiology*, 14, 784-790

Fehr, E & Schmidt, K.M (1999) A theory of fairness, competition and co-operation, *Quarterly Journal of Economics*, 114, 817-868

Gintis, H (2003) The hitchhiker's guide to altruism: Gene-culture co-evolution and internalization of norms, *Journal of Theoretical Biology*, 220, 407-418

Gintis, H; Smith, E.A & Bowles, S (2001) Costly signalling and co-operation, *Journal of Theoretical Biology*, 213, 103-119

Grier, J.W & Burk, T (1992) *Biology of Animal Behaviour*, Dubuque, IO: W.C.Brown

Gurven, M; Allen-Arave, W; Hill, K & Hurtado, M (2000) It's a wonderful life: Signalling generosity among the Ache of Paraguay, *Evolution and Human Behaviour*, 21, 263-282

Hamilton, W.D (1964) The genetic evolution of social behaviour I, II, *Journal of Theoretical Biology*, 7, 1-52

Hardin, G.J (1968) The tragedy of the commons, *Science*, 62, 1234-1248

Henrich, J (2004) Inequity aversion in capuchins? *Nature*, 428, p139

Herrnstein, R.J (1991) Experiments on stable sub-optimality in individual behaviour, *American Economic Review*, 81, 360-364

Hinde, R (1982) *Ethology*, Oxford: Oxford University Press

Howley, P (2002) *Breaking Spears and Mending Hearts*, London: Zed Books

Insel, T.R & Young, L.J (2001) The neurobiology of attachment, *Nature Reviews: Neuroscience*, 2, 129-136

Kosfeld, M; Heinrichs, M; Zak, P.J; Fischbacher, U & Fehr, E (2005) Oxytocin increases trust in humans, *Nature*, 435, 673-676

Krebs, D.L (1998) The evolution of moral behaviour. In Crawford, C & Krebs, D (eds) *Handbook of Evolutionary Psychology: Ideas, Issues and Applications*, Mahwah, NJ: Lawrence Erlbaum

Krebs, J & Davies, N (1993) *An Introduction to Behavioural Ecology* (3rd ed), Oxford: Blackwell

Kudadjie-Gyamfi, E & Rachlin, H (1996) Temporal patterning in choice among delayed outcome, *Organisational Behaviour and Human Decision Processes*, 65, 61-67

Laland, K & Brown, G (2002) *Sense and Nonsense*, Oxford: Oxford University Press

Latane, B & Darley, J.M (1970) *The Unresponsive Bystander: Why Doesn't He Help?* Englewood Cliffs, NJ: Prentice-Hall

LeVay, S (1993) *The Sexual Brain*, Cambridge, MA: MIT Press

Lippa, R (1994) *Introduction to Social Psychology* (2nd ed), Pacific Grove, CA: Brooks/Cole

Matthews, R (1998) Don't get even, get mad, *New Scientist*, 10/10, 26-31

Matthews, R (2000) We can work it out, *New Scientist*, 3/6, 36-40

Maynard Smith, J (1974) The theory of games and evolution of animal conflicts, *Journal of Theoretical Biology*, 47, 209-221

Maynard Smith, J (1982) *Evolution and the Theory of Games*, Cambridge: Cambridge University Press

Messick, D.M et al (1983) Individual adaptations and structural change as a solution to social dilemmas, *Journal of Personality and Social*

Psychology, 44, 294-309

Milinski, M; Semmann, D & Krambeck, H.J (2002) Reputation helps solve the "tragedy of the commons", *Nature*, 415, 424-426

Nesse, R (1999) Testing evolutionary hypotheses about mental disorders. In Stearns, S (ed) *Evolution in Health and Disease*

Nowak, M.A & Sigmund, K (1993) A strategy of win-stay-lose-shift that outperforms tit-for-tat in the prisoner's dilemma game, *Nature*, 364, 56-58

Nowak, M.A & Sigmund, K (1998) Evolution of indirect reciprocity by image scoring, *Nature*, 393, 573-577

Nowak, M.A & Sigmund, K (2005) Evolution of indirect reciprocity, *Nature*, 437, 1291-1298

Nowak, M.A; Sasaki, A; Taylor, C & Fudenberg, D (2004) Emergence of co-operation and evolutionary stability in finite populations, *Nature*, 428, 646-650

Packer, C; Scheel, D & Pusey, A (1990) Why lions form groups: Food is not enough, *American Naturalist*, 136, 1-19

Packer, C; Gilbert, D; Pusey, A & O'Brien, S (1991) A molecular genetic analysis of kinship and co-operation in African lions, *Nature*, 351, 562-565

Packer, C et al (1988) Reproductive success in lions. In Clutton-Brock, T (ed) *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*, Chicago: University of Chicago Press

Panchanathan, K & Boyd, R (2004) Indirect reciprocity can stabilise co-operation without the second-order free rider problem, *Nature*, 432, 499-502

Pennington, D (1999) Social dilemmas, *Psychology Review*, September, 2-5

Piliavin, J.A; Dovidio, J.F; Gaertner, S.L & Clark, R.D (1981) *Emergency Intervention*, New York: Academic Press

Rachlin, H (2002) Altruism and selfishness, *Behavioural and Brain Sciences*, 25, 2, 239-250

Rilling, J.K et al (2002) A neural basis for social co-operation, *Neuron*, 35, 395-405

Sanfey, A.G; Rilling, J.K; Aronson, J.A; Nystrom, L.E & Cohen, J.D (2003) The neural basis of economic decision-making in the ultimatum game, *Science*, 300, 1755-1758

Silk, J.B et al (2005) Chimpanzees are indifferent to the welfare of unrelated group members, *Nature*, 437, 1357-1359

Silverstein, A; Cross, D; Brown, J & Rachlin, H (1998) Prior experience and patterning in a prisoner's dilemma game, *Journal of Behavioural Decision Making*, 11, 123-138

Symons, D (1979) *The Evolution of Human Sexuality*, New York: Oxford University Press

Trivers, R (1971) Evolution of reciprocal altruism, *Quarterly Review of Biology*, 46, 35-37

Trivers, R (1985) *Social Evolution*, Reading, MA: Benjamin/Cummings

Walker, M (2001) Family comes first, *New Scientist*, 30/6, p21

Yagi, Y & Shimuzu, K (1996) Helping behaviour following a failure experience, *Japanese Psychological Review*, 38, 2, 53-65

Zahavi, A (1995) Altruism as a handicap - the limitations of kin selection and reciprocity, *Journal of Avian Biology*, 26, 1-3